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Flood pulse influence on the feeding ecology of two Amazonian auchenipterid catfishes

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We assessed the flood pulse effect on the diet composition, trophic niche breadth, and the amount of food intake of two Amazonian auchenipterids with different feeding strategies. Sampling was carried out quarterly (from April/2012 to January/2014) on the middle Xingu River, using gillnets. We measured specimens for standard length and total weight. The specimens' stomachs were removed, weighed, and had their contents identified. We analyzed 360 stomachs of *Auchenipterus nuchalis* and 584 of *Tocantinsia piresi*. The diet of *A. nuchalis* was mainly composed of aquatic insects and crustaceans, while *T. piresi* fed on fruits and seeds. The diet composition of both species varied seasonally, but only *T. piresi* changed its trophic niche breadth in response to hydrological changes, becoming more specialist during the higher water periods (filling and flood). Both species also showed differences in their amount of food intake between hydrological periods, with *A. nuchalis* feeding more intensely in lower water periods (ebb and dry), while *T. piresi* in the higher water periods. We evidenced different responses to the hydrological periods for the related species. We emphasize that studies considering the relationship between flood pulse and feeding ecology of the organisms are essential to understanding river floodplain systems' dynamics.

Keywords: Amazon basin, Diet, Niche breadth, Siluriformes, Xingu River.

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Avaliamos o efeito do pulso de inundação na composição da dieta, amplitude de nicho trófico e quantidade de alimento ingerido de dois auchenipterídeos amazônicos com diferentes estratégias alimentares. Os espécimes foram amostrados trimestralmente entre abril/2012 e janeiro/2014 no médio rio Xingu, utilizando malhadeiras. Estes foram mensurados quanto ao comprimento padrão e peso total. Os estômagos dos espécimes foram removidos, pesados e seu conteúdo identificado. Analisamos 360 estômagos de *Auchenipterus nuchalis* e 584 de *Tocantinsia piresi*. A dieta de *A. nuchalis* foi predominantemente composta por insetos aquáticos e crustáceos, enquanto para *T. piresi* frutos e sementes predominaram. A composição da dieta de ambas as espécies variou sazonalmente, mas apenas para *T. piresi* a amplitude de nicho trófico variou entre períodos hidrológicos, sendo mais especialista nos períodos de águas altas (enchente e cheia). Ambas as espécies diferiram na quantidade de alimento ingerido entre os períodos hidrológicos, sendo maior para *A. nuchalis* nos períodos de águas baixas (vazante e seca) e para *T. piresi* nos períodos de águas altas. Evidenciamos diferentes respostas à variação hidrológica pelas espécies. Enfatizamos que estudos considerando a relação entre a dinâmica do pulso de inundação e a ecologia alimentar dos organismos é fundamental para um melhor entendimento da dinâmica das planícies de inundação.

Palavras-chave: Amplitude de nicho, Bacia Amazônica, Dieta, Rio Xingu, Siluriformes.

INTRODUCTION

Flood pulse is the main ecological driver of freshwater floodplain rivers (Junk *et al*., 1989; Thomaz *et al*., 2007). Many terrestrial and aquatic organisms depend on this hydrological dynamic for food supply, breeding, and shelter (Ocock *et al*., 2014; Robinson, Pizo, 2017; Bayley *et al*., 2018). These organisms have developed specific behavioral strategies to use periodically available habitats and resources during high and low water periods (Alho, Sabino, 2012; Naus, Reid Adams, 2018). For fish fauna, the flood pulse plays a significant role in reproduction and feeding strategies (Bailly *et al*., 2008; Luz-Agostinho *et al*., 2008; Barbosa *et al*., 2018), as well as in their assemblage structure (Barbosa *et al*., 2015; Fitzgerald *et al*., 2018). In the tropics, the high fish diversity is accompanied by a high diversity of ecological strategies, presenting different responses to these periodic environmental changes (Lowe-McConnell, 1987).

New foraging areas become available during flood periods, and so do new food resources, such as fruits, seeds, and terrestrial insects that drop into the water from the forest canopy while others become more difficult to find (Lowe-McConnell, 1987; Correa, Winemiller, 2014; Castello, Macedo, 2016). The more extensive availability of energetically rich food resources in the high-water periods is advantageous for many fish species that explore the floodplains for feeding (Goulding, 1980; Correa *et al*., 2007; Mortillaro *et al*., 2015; Costa-Pereira, 2017). Based on the Optimal Foraging Theory (MacArthur, Pianka, 1966), the organism tends to have a more specialized diet searching for food that optimizes their energy gain during this period. For instance, invertivorous and frugivorous species have their diet based mainly on allochthonous resources (Freitas *et al*., 2011). Contrary, in the low water periods, the diet of these trophic groups becomes predominantly dependent on autochthonous food items (Lopes *et al*., 2017). Thus, the flood pulse has a tangible role in fish's ecology (Junk *et al*., 1989), especially in their feeding strategies adjustment for a more efficient use of available resources (MacArthur, Pianka, 1966).

Knowledge about the feeding dynamics of the fish species may provide an essential baseline for understanding their role in aquatic ecosystems (Winemiller, 1989), and such ecological data are desirable for environmental conservation. While the influence of hydrological cycles on the feeding strategies of fish is well-documented (Mérona *et al*., 2001; Prudente *et al*., 2016; Dary *et al*., 2017), this knowledge is far from being comprehensive, given the high fish diversity in the Neotropical region, especially in the Amazon Basin (Reis *et al*., 2016). For Auchenipteridae catfishes, for instance, the knowledge gaps on feeding habits [see Raunkiæran shortfalls in Hortal *et al*. (2015)] are noteworthy, and information about their diet is still accumulating with every new study published (Freitas *et al*., 2021).

The Xingu River is an important tributary on the right bank of the Amazon River, widely known for its complex geomorphology resulting in rapids and anastomosing channels (Fitzgerald *et al*., 2018). It also harbors a fish diversity with high rates of endemism (Dagosta, De Pinna, 2019), many of them important in artisanal fisheries (Issac *et al*., 2015) and ornamental fish trade (Ramos *et al*., 2015). The species of the present study, the auchenipterids *Auchenipterus nuchalis* (Spix & Agassiz, 1829) and *Tocantinsia piresi* (Miranda Ribeiro, 1920), are among the most abundant species of the middle Xingu River, being considered relevant ecological models to advance the understanding of the effect of river fluviometric dynamics on the trophic ecology of fish in this region. In addition, these species were also considered a target species in the Basic Environmental Plan, which is used to support mitigation and compensatory actions for environmental impacts identified during the environmental licensing process for the construction of the Belo Monte Dam. In previous studies, *A. nuchalis* and *T. piresi* were described as insectivorous (Pouilly *et al*., 2004; Mérona, Vigouroux, 2006) and insectivorous/frugivorous (Carvalho, Kawakami, 1984; Dary *et al*., 2017), respectively. Considering that this region was recently affected by one of the most controversial hydropower plants in the Amazon, the Belo Monte (concluded in November 2015), our research provides novel ecological data before the complete Xingu River damming.

In this sense, we aimed to evaluate how the water level variation in the middle Xingu River affects the feeding ecology of *A. nuchalis* and *T. piresi.* We expected a higher contribution of allochthonous resources in the diet composition, lower niche breadth, and greater feeding intensity during high water periods for both species.

MATERIAL AND METHODS

Study area. The study was carried out on the middle Xingu River (03°12'52"S 52°11'23"W) – a right-bank tributary of the Amazon River – and in their tributaries Bacajá River (03°45'12"S 51°34'59"W) and Iriri River (03°49'33"S 52°41'36"W) (Fig.

1). Known as "Volta Grande", this section of the Xingu River basin is characterized by clear water with high flow over a bedrock. This region presents a marked fluviometric variation, with water levels increasing by 5 m during the flood season, creating larges floodplain areas. During the studied period (from April 2012 to January 2014), the local monthly precipitation and water level ranged from 10.8 mm to 478.3 mm (INMET, 2014) and 245 cm to 737 cm (ANA, 2018), respectively. Thus, we considered four distinct hydrological periods: flood (between March and May), ebb (June–August), dry (September–November), and filling (December and February), as previously defined by Freitas *et al*. (2015). These hydrological periods were herein used as a proxy to flood pulse dynamics (Fig. **S1**).

Sampling sites. Fishes were sampled quarterly between April 2012 and January 2014, totaling eight field expeditions, with each hydrological season being assessed twice. We defined ten areas separated by approximately 40 km in the fluvial distance (Fig. 1), which, when sampled quarterly results in 80 sampling sites (ss). In each sampling site, three sets of gillnets of monofilament nylon (meshes of 2, 4, 7, 10, 12, 15, and 18 cm) with 100 m-long and two m-height (each) were disposed for twelve hours and harvested every six hours. When sampled alive, the specimens were anesthetized using clove oil (Fernandes *et al*., 2017).

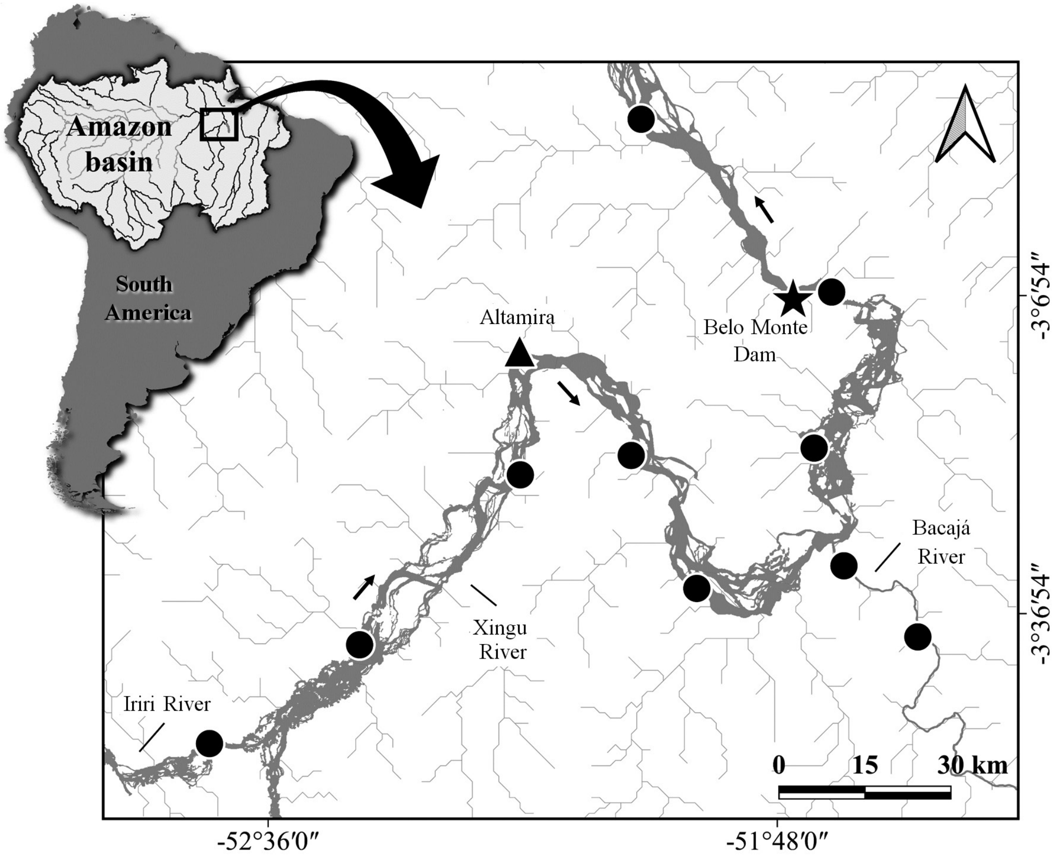

FIGURE 1 | Study area on the middle Xingu River (Eastern Amazon, Brazil). The black dots represent the sampling sites, and the arrows indicate the direction of the water flow. Black triangle = Altamira municipality; black star = Belo Monte Dam.

Standard length (SL, cm), total weight (WT, g), and stomach weight (WS, g) were measured for all collected specimens of *A. nuchalis* and *T. piresi*. Voucher specimens were fixed in 10% formalin solution for approximately 48h, transferred to 70% ethanol, and deposited at the Laboratório de Ictiologia de Altamira (LIA), Universidade Federal do Pará (UFPA), municipality of Altamira, Pará State, Brazil, under the code: LIA 363 for *A. nuchalis* and LIA 383 for *T. piresi*.

Stomach contents were identified to the lowest taxonomic level possible using specialized literature (Costa *et al*., 2006; Hamada, Ferreira-Keppler, 2012) and expert assistance, and weighed (precision of 0.001 g). For each food item, the frequency of occurrence (FO%; Hyslop, 1980) and mass percentage (M%; Hynes, 1950) were calculated, and then combined into the Alimentary Index (Ai%; changed from Kawakami, Vazzoler, 1980), which attributed the importance of each item in the fish diet. The Ai% was calculated by the equation, $Ai\% = (FO\% \times M\%/\sum FO\% \times M\%) \times 100$. Food items were grouped into ten categories: Algae, Aquatic insects, Arachnids, Crustaceans, Fish, Fruit and seeds, Mollusks, Other plant fragments (*e.g*., branches, leaves, and flowers), Terrestrial insects, and Terrestrial vertebrates, which also had their respective values of Ai% calculated.

Data analysis. For both species, variation in diet composition between hydrological periods was assessed using a Principal Coordinates Analysis (PCoA) based on a Bray-Curtis similarity matrix of the log-transformed categorical Ai% values and tested using a global and pairwise Permutational Multivariate Analysis of Variance (PERMANOVA). This analysis was followed by a similarity percentage analysis (SIMPER) to determine the diet category responsible for diet dissimilarity among the hydrological periods. For PCoA and PERMANOVA, we grouped the different years in the hydrological periods, considered only hydrological periods represented by at least three sampling sites and sampling sites with at least two non-empty stomachs, minimal numbers required to carry out the statistical test and obtain the alimentary index, respectively.

To verify if the origin of the resource consumed by the species varied between hydrological periods, food items were grouped into autochthonous (originates from the aquatic environment) and allochthonous resources (from the terrestrial environment), and then had their alimentary index (Ai%) calculated. These values were visually examined against the hydrological period.

Trophic niche breadth was assessed by testing homogeneity of dispersion in diet composition (PERMDISP, Permutational Analysis of Multivariate Dispersion), a dissimilarity-based multivariate extension of Levene's test (Anderson *et al*., 2008). This test is based on the ANOVA F statistic, which compares the average distances from observed values and their centroid. Greater dispersion values indicate greater niche amplitude. PCoA, PERMANOVA, and PERMDISP analyses were performed in the statistical software PRIMER 6 (Clarke, Gorley, 2006) with PERMANOVA+1.0.3 package (Anderson *et al*., 2008).

Differences in the total amount of food intake between hydrological periods were evaluated using the Repletion Index (RI%), given by the equation $RI\% = (WS/WT) \times 100$ (Santos, 1979), where WS is the stomach weight and WT is the total weight. Considering that these data did not meet the assumptions of parametric tests, RI% values were tested using a Kruskal-Wallis (H) test followed by a Mann-Whitney pairwise comparison test (Zar, 2010). Finally, the relationship between the amount of ingested food (RI% values) and average fluviometric quotas [obtained from ANA (2018)] was assessed based on a beta regression analysis (using *betareg* package in R environment). It assumes that response variables are proportions or percentages values and are beta distributed (Cribari-Neto, Zeileis, 2010). Visual inspection of the residuals validated the *betareg* model. Finally, empty stomachs were not considered in any previous analysis. All statistics tested were carried out considering a significance level of 0.05 (Zar, 2010).

RESULTS

A total of 360 stomachs of *A. nuchalis* and 584 *T. piresi* were analyzed, of which 221 and 333 had stomach content, respectively. The standard length of *T. piresi* ranged from 9.3 to 46.0 cm (mean = 31.3; standard deviation = 5.3), and for *A. nuchalis* ranged from 8.1 to 19.5 cm (mean = 12.4; standard deviation = 2.0). Based on the criteria of sampling site selection (see Material and methods), the diet composition was analyzed considering 16 sampling sites for *A. nuchalis* and 28 sampling sites for *T. piresi*. The number of stomachs and sampling sites assessed by season/year for *A. nuchalis* and *T. piresi* are shown in Tabs. 1–2, respectively.

The diet of *A. nuchalis* was composed of 27 food items (Tab. 1), primarily autochthonous items such as aquatic insects (76.0 Ai%) and crustaceans (16.5 Ai%). The first two axes of the principal coordinate analysis (PCoA) explained 53.4% and 29.1% of the total variation in the diet composition of *A. nuchalis*, respectively (Fig. 2A). We observed variation in diet composition among the hydrological periods (Pseudo-F = 3.303, p = 0.012), with a significant difference between dry and filling seasons (p = 0.024). According to the SIMPER analysis, the average dissimilarity between these seasons was equal to 71.52%. It was mainly influenced by the consumption of crustaceans (percentage of contribution = 30.78%), followed by aquatic insects (30.69%) and terrestrial insects (27.57%). The contribution of the other categories was less than 11%.

The diet of *A. nuchalis* was predominantly composed of crustaceans during the dry season in 2012 (99.77 Ai%) (Fig. 2B) and aquatic insects during the dry season in 2013 (99.99 Ai%), while in the filling season in 2013 and 2014 the diet was composed by aquatic insects (62.64 and 75.0 Ai%, respectively), and terrestrial insects (25.46 and 22.96 Ai%, respectively) (Figs. 2C, D). During the food season in 2012 and 2013, the diet was mainly composed by aquatic insects (59.20 and 90.29 Ai%, respectively). The ebb was not included in the PERMANOVA analysis because it was represented by only two sampling sites (Tab. 1). In this period, we analyzed 13 stomachs of *A. nuchalis*, recording a diet mainly composed of crustaceans (94.35 Ai%). No specimen of *A. nuchalis* was caught in the ebb 2013.

For *T. piresi*, the diet was composed of 30 food items (Tab. 2), with high consumption of fruit and seeds (98.17 Ai%). The first two axes of PCoA explained 58.4% and 20.2% of the diet composition of *T. piresi*, respectively (Fig. 3A). As for *A. nuchalis*, the diet of *T. piresi* differed between hydrological periods (Pseudo-F = 6.073, p = 0.001) (Tab. 3). Differences in diet composition were observed between flood and ebb season (p = 0.0332) and between filling and ebb season (p = 0.009). The SIMPER analysis evidenced an average dissimilarity of 65.41% between flood and ebb season, which was influenced essentially

TABLE 1 | Alimentary Index (Ai%) of food items in the diet of *Auchenipterus nuchalis* from the Xingu River, Eastern Amazon, Brazil. n = number of stomachs evaluated. ss = number of sampling sites. The food categories are shown in bold.

Food Items	2012			2013				2014	Total
	Flood (n=12) (ss=1)	Ebb (n=13) (ss=2)	Dry (n=18) (ss=2)	Filling (n=41) (ss=4)	Flood (n=56) (ss=3)	Ebb (n=0) (ss=0)	Dry (n=32) (ss=1)	Filling (n=46) (ss=3)	
ALLOCHTHONOUS									
Arachnid					**<0.01**			**<0.01**	**<0.01**
Araneae					<0.01			<0.01	<0.01
Acari									<0.01
Terrestrial insects	**33.72**	**5.46**	**0.23**	**25.46**	**9.52**			**22.96**	**7.40**
Blattaria					0.85				0.04
Coleoptera adult	19.71	2.10		3.40	1.06			2.63	1.63
Diptera adult	0.32	0.38	0.27	<0.01				1.33	0.26
Odonata adult								0.18	<0.01
Hymenoptera (Formicidae)	14.06	0.01	<0.01	<0.01	6.30			1.05	1.05
Isoptera	1.52				<0.01			0.76	0.05
Trichoptera adult				0.01				0.50	0.02
Terrestrial insect fragments				19.59	0.55			1.22	1.43
AUTOCHTHONOUS									
Aquatic insects	**59.20**	**0.19**		**62.64**	**90.29**		**99.99**	**75.00**	**76.00**
Coleoptera larvae	0.21				<0.01			0.64	0.02
Diptera larvae				0.76	12.56		99.99	0.43	58.53
Ephemeroptera larvae	0.60			50.07	4.40			82.24	11.01
Hemiptera larvae					0.21			4.59	0.20
Heteroptera larvae					0.10				0.00
Neuroptera larvae	9.52				0.12				0.04
Odonata larvae	1.11	0.13			6.56				0.52
Plecoptera larvae					0.10				<0.01
Trichoptera larvae	23.88			0.05	0.00			0.03	0.08
Aquatic insect fragments	13.95			2.93	66.58			0.33	5.12
Crustaceans	**7.08**	**94.35**	**99.77**	**11.14**	**0.19**		**0.01**	**0.85**	**16.50**
Amphipoda	15.11	97.39	85.34						17.17
Cladocera								0.01	<0.01
Decapoda (Brachyura)								0.10	<0.01
Decapoda (Caridea)								0.68	0.02
Ostracoda			0.38	21.71	0.60		0.01		2.01
Crustacean fragments			14.00						0.52
Fish			**<0.01**	**0.76**				**1.19**	**0.10**
Fish scale			<0.01	1.49				3.28	0.28

by the consumption of fruits and seeds (percentage contribution = 29.50%), followed by fishes (19.73%) and aquatic insects (17.75%). The average dissimilarity between filling and ebb season was 60.59%, with a higher percentage contribution from the consumption of fruits and seeds (28.90%), followed by aquatic insects (17.73%) and fishes (17.29%). The other categories presented a percentage contribution of less than 15.5%

Although fruits and seeds were predominant in all hydrological seasons (Fig. 3B), the diet of *T. piresi* in the ebb 2013 was mainly composed of aquatic insects (91.95 Ai%)

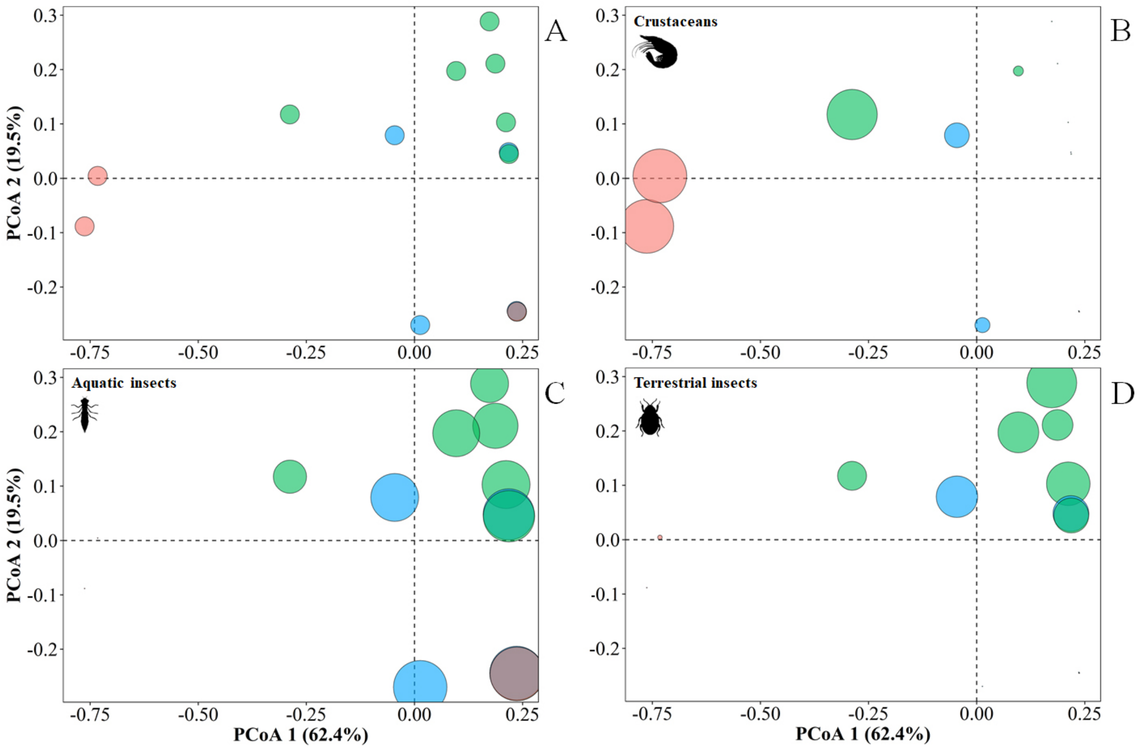

FIGURE 2 | Graphic representation of the Principal Coordinates Analysis (PCoA) of the diet composition of *Auchenipterus nuchalis* (**A**) from the Xingu River (Eastern Amazon, Brazil). Colors represent the hydrological seasons: flood (blue), dry (red), and filling (green). The contribution of the main food items is expressed according to the circle size (**B** – terrestrial insects; **C** – aquatic insects; and **D** – crustaceans). The purple color represents an overlap of dry and flood samples.

(Fig. 3C). The dry season was not considered in the PERMANOVA analysis; only two sampling sites (and four stomachs) represented the dry 2012 (Tab. 2). In this period, the diet was composed of fish (37.57 Ai%) (Fig. 3D), aquatic insects (37.40 Ai%), and terrestrial insects (24.87 Ai%). We caught no specimen of *T. piresi* in the dry 2013.

Regarding the origin of the food items, the diet of *A. nuchalis* was composed of 80% of autochthonous items throughout the studied period (Fig. 4A). On the other hand, the diet of *T. piresi* was highly changeable during the study period. During the higher water periods (flood and filling periods) and the ebb 2012, the diet of *T. piresi* was composed of more than 90% of allochthonous items. Elseways, autochthonous items were the primary food source (more than 90%) during the dry 2012 and ebb 2013 (Fig. 4B).

Differences in trophic niche breadth between hydrological periods (PERMDISP analysis) were not significant for *A. nuchalis* (F = 0.192, p = 0.828), but were significant for *T. piresi* (F = 6.151, p = 0.006), with differences between flood and ebb seasons (t = 5.619; p = 0.001), and ebb and filling (t = 3.187; p = 0.005) (Tab. 3). The PERMDISP result of *T. piresi* suggests a more specialist feeding strategy during the flood and filling seasons (centroid distance; cd = 0.103 and 0.191, respectively), against a more generalist feeding habit in the ebb season (cd = 0.425) (Tab. 3). The dry season was not considered in the PERMDISP analysis based on the sampling site selection criteria.

The amount of food eaten (RI%) by *A. nuchalis* differed in relation to the hydrological periods assessed ($H_{6,\,0.05} = 33.95$; $p < 0.001$; Fig. 5B). The highest levels of feed intensity

TABLE 2 | Alimentary Index (Ai%) of food items in the diet of *Tocantinsia piresi* from the Xingu River, Eastern Amazon, Brazil. n = number of stomachs evaluated. ss = number of sampling sites. The food categories are shown in bold.

Food Items	2012			2013				2014	Total
	Flood (n=75) (ss=5)	Ebb (n=2) (ss=1)	Dry (n=4) (ss=1)	Filling (n=69) (ss=8)	Flood (n=61) (ss=4)	Ebb (n=27) (ss=2)	Dry (n=0) (ss=0)	Filling (n=95) (ss=7)	
ALLOCHTHONOUS									
Fruit and seeds	**99.61**	**85.99**		**84.71**	**99.04**	**0.03**		**99.31**	**98.17**
Fruits and seeds	99.76	85.99		92.62	99.44	0.03		99.47	98.95
Other plant fragments	**0.08**		**0.16**	**0.03**	**0.42**	**1.22**		**0.04**	**0.15**
Branch	0.03			0.02	0.12	0.31		0.02	0.05
Flower	0.02				0.01	0.05		<0.01	0.01
Leaf	<0.01		0.19	<0.01	0.05	0.20		<0.01	0.01
Terrestrial insects	**0.04**		**24.87**	**1.45**	**0.01**	**0.33**			**0.07**
Coleoptera adult	<0.01		8.03	0.28		<0.01		<0.01	0.01
Coleoptera larvae	<0.01			<0.01					<0.01
Diptera	<0.01								<0.01
Hemiptera						<0.01			<0.01
Hymenoptera			3.46	0.09					<0.01
Lepidoptera	<0.01				<0.01				<0.01
Mantodea						<0.01			<0.01
Orthoptera	0.01			0.02	0.01	0.01			0.01
Phasmatodea	<0.01								<0.01
Terrestrial vertebrates				**0.02**	**<0.01**	**<0.01**			**<0.01**
Amphibia (Anura)					<0.01				<0.01
Birds (Feather)						<0.01			<0.01
Squamata (Colobridae)				0.03					<0.01
AUTOCHTHONOUS									
Algae	**0.01**					**<0.01**			**<0.01**
Algae	0.01					<0.01			<0.01
Aquatic insects	**0.01**		**37.40**	**<0.01**		**91.95**			**0.46**
Ephemeroptera larvae	<0.01								<0.01
Hemiptera						96.55			0.36
Megaloptera larvae			44.06						<0.01
Odonata larvae	<0.01			<0.01		<0.01			<0.01
Crustaceans	**0.22**			**3.24**	**0.44**	**1.23**		**0.34**	**0.51**
Decapoda (Brachyura)	0.15			3.13	0.34	1.29		0.34	0.43
Decapoda (Caridea)	0.01			<0.01	<0.01				<0.01
Mollusks				**0.03**		**0.01**			**<0.01**
Bivalvia						<0.01			<0.01
Gastropoda				0.03		0.01			<0.01
Fish	**0.05**	**14.01**	**37.57**	**10.52**	**0.09**	**5.23**		**0.31**	**0.64**
Characiformes	0.01			0.23	0.01	0.12		0.14	0.06
Gymnotiformes					0.01				<0.01
Siluriformes				1.67		1.04			0.03
Synbranchiformes						0.28			<0.01
Fish fragments	0.01	14.01	44.25	1.89	<0.01	<0.01		0.03	0.07

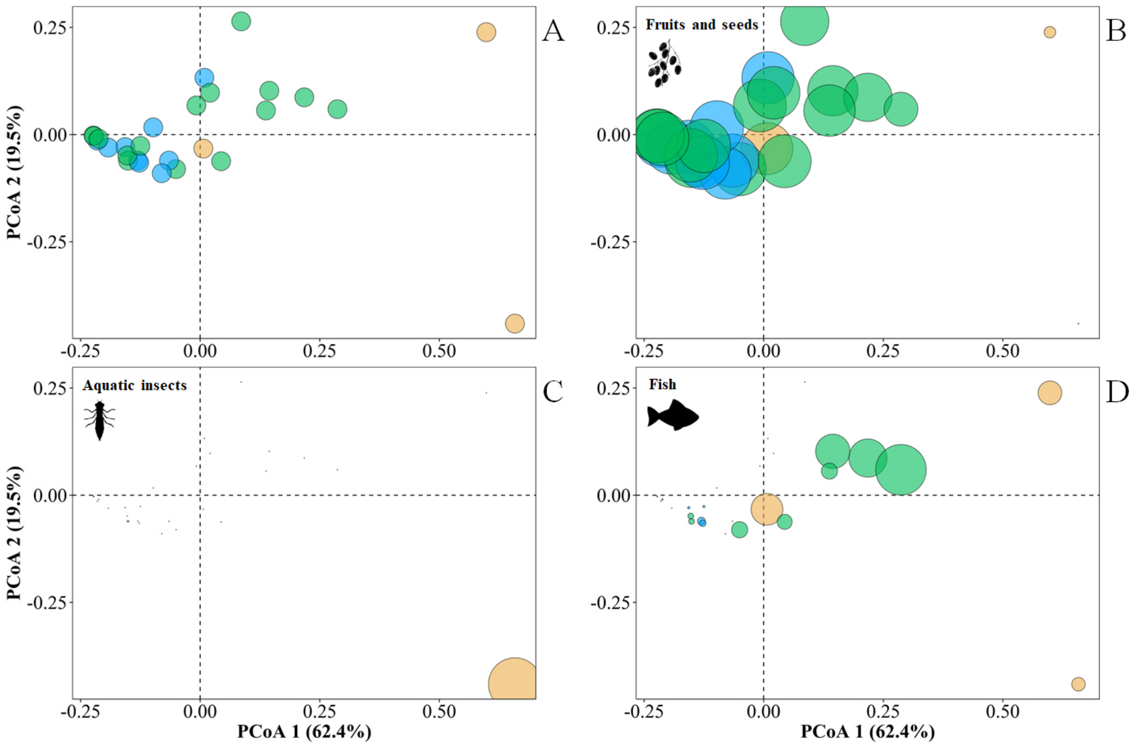

FIGURE 3 | Graphic representation of the Principal Coordinates Analysis (PCoA) of the diet composition of *Tocantinsia piresi* (**A**) from the Xingu River (Eastern Amazon, Brazil). Colors represent the hydrological seasons: flood (blue), ebb (yellow), and filling (green). The contribution of the main food items is expressed according to the circle size (**B** – fruits and seeds; **C** – aquatic insects; and **D** – fish).

TABLE 3 | Statistical values for the diet composition (PERMANOVA and PERMDISP) of *Auchenipterus nuchalis* and *Tocantinsia piresi* from the Xingu River, Eastern Amazon, Brazil. *Statistical differences.

Species	Periods (Centroid distance)	PERMANOVA				PERMDISP			
		Global		Pairwise		Global		Pairwise	
		PseudoF	p-value	t	p-value	F	p-value	t	p-value
Auchenipterus nuchalis	Flood (0.173)/ Dry (0.343)	3.805	0.019*	1.705	0.194	0.558	0.740		
	Flood (0.173)/ Filling (0.200)			1.356	0.197				
	Dry (0.343)/ Filling (0.200)			2.312	0.021*				
Tocantinsia piresi	Flood (0.103)/ Ebb (0.425)	6.316	0.002*	3.098	0.012*	10.087	0.003*	5.619	0.001*
	Flood (0.103)/ Filling (0.191)			1.628	0.061			1.858	0.098
	Ebb (0.425)/ Filling (0.191)			2.579	0.021*			3.187	0.005*

were registered during the dry 2012 (mean RI% = 0.50; standard deviation = 0.74) and dry 2013 (0.32 ± 0.61), and the lowest values of RI% were in the flood 2012 (0.07 ± 0.06) and flood 2013 (0.08 ± 0.15). However, differences were only observed when we compared the RI% values of dry 2013 with the periods filling 2013 ($p = 0.001$), flood 2013 ($p < 0.001$), and filling 2014 ($p = 0.004$) (Tab. 4).

For *T. piresi*, RI% values also differed between hydrological periods ($H_{6,\ 0.05} = 68.76$; $p < 0.001$; Fig. 5B). The highest levels of feed intensity were registered during the flood 2012 (mean RI% = 4.38 ± 4.33) and filling 2014 (2.66 ± 2.64), and the lowest values of

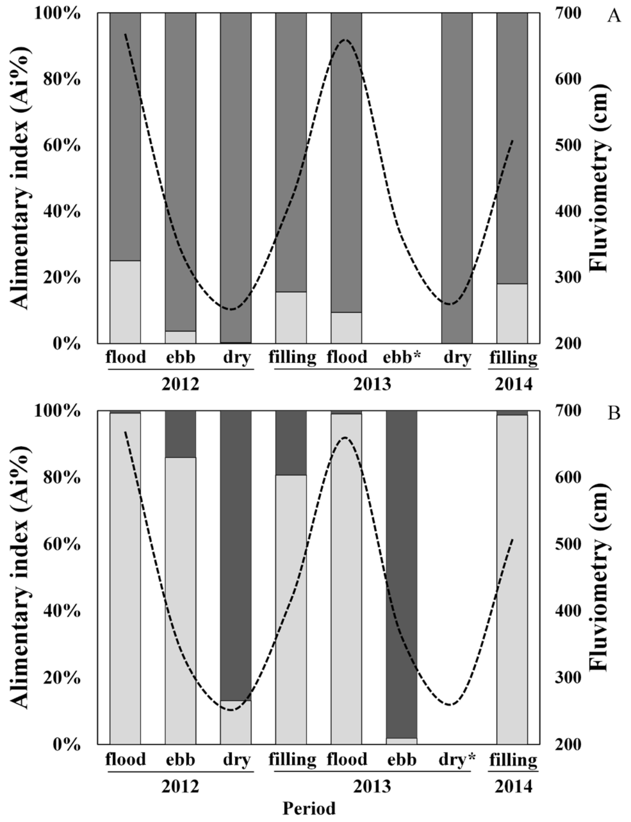

FIGURE 4 | Alimentary index (Ai%) values of the autochthonous (dark gray) and allochthonous (light gray) items of the diet of *Auchenipterus nuchalis* (**A**) and *Tocantinsia piresi* (**B**) from the Xingu River (Eastern Amazon, Brazil). The dotted line represents the fluviometric variation. Asterisks indicate the months which was not obtained the minimal specimens numbers required to obtain the alimentary index.

TABLE 4 | Pairwise comparison of Repletion Index (RI%) of *Auchenipterus nuchalis* and *Tocantinsia piresi* from the Xingu River, Eastern Amazon, Brazil. *Statistical differences.

MannWhitney pairwise comparison			2012			2013				2014
			Flood	**Ebb**	**Dry**	**Filling**	**Flood**	**Ebb**	**Dry**	**Filling**
Auchenipterus nuchalis	**2012**	**Flood**		1.000	1.000	1.000	1.000		0.785	1.000
		Ebb			1.000	0.870	0.142		1.000	1.000
		Dry				1.000	0.189		1.000	1.000
	2013	**Filling**					1.000		0.001*	1.000
		Flood							0.000*	1.000
		Ebb								
		Dry								0.004*
Tocantinsia vpiresi	**2012**	**Flood**		0.887	0.003*	0.000*	0.000*	0.014*		1.000
		Ebb			1.000	1.000	1.000	1.000		1.000
		Dry				1.000	0.443	0.578		0.020*
	2013	**Filling**					0.586	1.000		0.000*
		Flood						1.000		0.052
		Ebb								0.479
		Dry								

RI% were in the dry 2012 (0.05 ± 0.05) and flood 2013 (0.35 ± 0.35). During the flood 2012, this species presented a higher feeding intensity when compared to almost all studied periods, except ebb 2012 and filling 2014 (all $p < 0.05$; see Tab. 4). Repletion values also differed between filling 2014 and dry 2012 ($p = 0.020$), and filling 2012 ($p < 0.001$) (Tab. 4).

Additionally, the beta regression model showed a weak relationship between the feeding intensity and fluviometric quota for both species. The RI% values of *A. nuchalis* were negatively related to the fluviometry (estimate = –0.001, Z = –2.873, df = 3, $p = 0.004$; Pseudo R^2= 0.061) (Fig. 5C). Otherwise, the RI% values of *T. piresi* were positively related to the fluviometry (estimate = 0.001, Z = 3.853, df = 3, $p < 0.001$; Pseudo R^2= 0.062) (Fig. 5D). The highest feeding intensity was registered in the flood 2012 (mean RI% = 4.38 ± 4.33) and filling 2014 seasons (mean RI% = 2.66 ± 2.64), and the lowest values of RI% were in the dry 2012 season (mean RI% = 0.05 ± 0.05) and ebb 2012 period (mean RI% = 0.35 ± 0.35). The Fig. 6 shows an infographic summary of the results obtained herein.

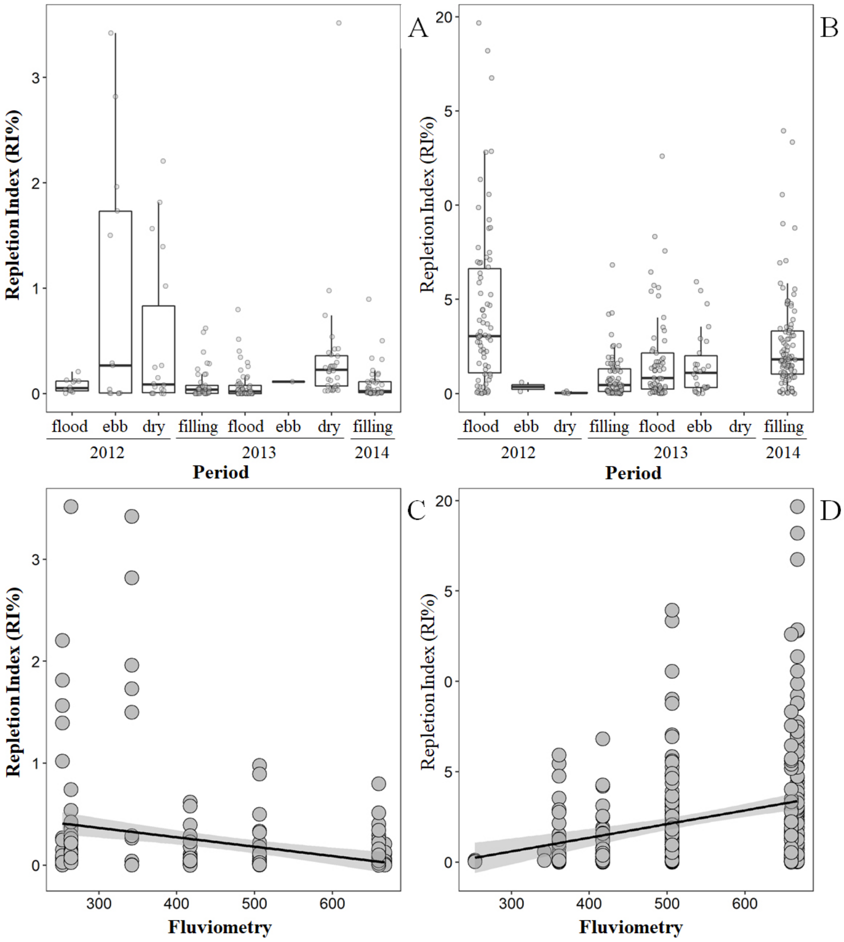

FIGURE 5 | Variation in the Repletion Index (RI%) of *Auchenipterus nuchalis* (**A–C**) and *Tocantinsia piresi* (**B–D**) from the Xingu River (Eastern Amazon, Brazil). Black line represents the linear regression model (**C–D**).

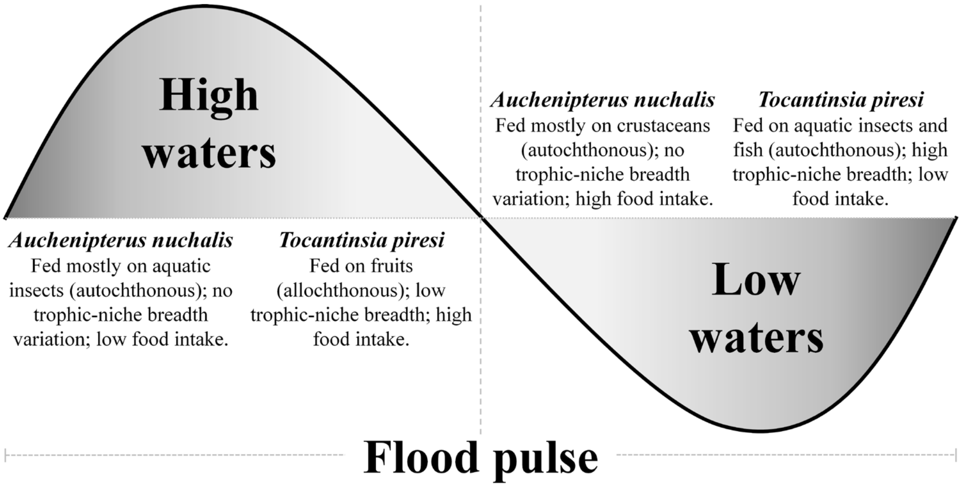

FIGURE 6 | Infographic summarizing the feeding ecology of *Auchenipterus nuchalis* and *Tocantinsia piresi* from the Xingu River, Eastern Amazon, Brazil.

DISCUSSION

The diet analysis revealed an invertivorous habit for *Auchenipterus nuchalis*, feeding primally on autochthonous insects and crustaceans, and can be considered an invertivore species, predominantly consuming invertebrates of autochthonous origin, with higher food intake during dry seasons. For *Tocantinsia piresi*, the feeding habit was omnivorous, with a predominantly frugivorous habit, manly during the high water periods, and aquatic insects and fish during the low water periods. This fact highlighted a specialized trophic niche breadth of *T. piresi* during the flood season and generalist habits during the low water periods. Additionally, the highest food intake also occurred in higher water periods.

The insectivorous diet of *A. nuchalis* observed in the present study was also recorded in the central Amazon floodplains, in the confluence of the Amazon and Negro rivers (Mérona, Rankin-de-Mérona, 2004), as well as in the lower Tocantins River, which is affected by the Tucuruí Dam in the Eastern Amazon (Mérona *et al*., 2001). In the latter study, changes in the diet composition of *A. nuchalis* occurred because of the reservoir closure; before the dam closure, the diet was insectivore, and after the river closure, the feeding habit of this species changed to that of an unspecialized carnivore (Mérona *et al*., 2001). Likewise, the tendency of a frugivorous feeding habit recorded in the present study for *T. piresi* was previously described in a mid-course of the Teles Pires River (Tapajós basin), where the species showed a predominance in the consumption of vascular plants and fish (Dary *et al*., 2017). These studies reinforce the variety of feeding habits among auchenipterids fishes.

Both species varied their diet composition in response to changes in hydrological periods. However, the flood pulse had a different influence on the feeding ecology of these auchenipterids. The more significant interaction between the aquatic and terrestrial ecosystem promoted by the rising of the water level (Junk *et al*., 1989) did not increase allochthonous sources in the diet of *A. nuchalis*. However, we presume that the floodplain areas formed by the river flooding may affect the abundance, distribution, and life cycle of many benthic macroinvertebrate assemblages, including the prey species consumed by *A. nuchalis*, such as aquatic insects and crustaceans (McClain, 2002; Wantzen *et al*., 2016; Piniewski *et al*., 2017). In contrast, changes in the feeding ecology of *T. piresi* can be directly associated with local flood pulse. This species fed profusely on fruits and seeds of terrestrial plants in the periods of higher water levels, during which several plant species are bearing mature fruit (Maia, Jackson, 2000). This allochthonous resource is considered an important energy source for many Amazonian fishes (Goulding, 1980; Correa *et al*., 2007). In this context, *T. piresi* consumes as many fruits as possible during the floods to store energy for gonadal maturation, which occurs at the lower water periods (Freitas *et al*., 2015). In the dry season, when seeds and fruits are no longer available, *T. piresi* inhabit burrows in riverbed rocks (Freitas *et al*., 2015) and change the diet to aquatic insects and fish.

Other auchenipterid species has also been studied concerning the trophic ecology and the flood pulse dynamics; *Auchenipterichthys longimanus* (Günther, 1864) had more food intake in the flood period when fruits were abundant (Freitas *et al*., 2011); *Trachelyopterus galeatus* (Linnaeus, 1766) consumed mainly allochthonous items during the flood period such as terrestrial insects and fruits (Santos, 2005; Garcia *et al*., 2020); and *Ageneiosus apiaka* Ribeiro, Rapp Py-Daniel & Walsh, 2017 shifted from aquatic insects to crustaceans when the water level starts to rise (Dary *et al*., 2017). Despite the studies mentioned above, information on how hydrological changes affect feeding ecology of auchenipterid species remains scarce (*e.g*., Andrian, Barbieri, 1996; Santos, 2005; Freitas *et al*., 2011).

Many studies highlight the importance of flooded areas, their vegetation for aquatic communities, the diversity of different food and/or prey items available in these temporary habitats, and the flexibility in fish responses to spatial and temporal patterns in food source availability (Mortillaro *et al*., 2015; Pereira *et al*., 2017; Pool *et al*., 2017; Barbosa *et al*., 2018). The role of the flood pulse is also associated with other ecological aspects worldwide, such as the increase of fish recruitment during periods with higher water levels (Linhoss *et al*., 2012) and structuring fish assemblages (Gomes *et al*., 2012; Barbosa *et al*., 2015). Specific effects in local assemblages, or species, are far away from being fully unraveled.

Concerning niche breadth, only *T. piresi* presented a distinct feeding strategy between hydrological periods. During the flood period, the more specialist habit was determined by higher consumption of a single food item (fruits). Besides a high energetic value (Goulding, 1980; Correa *et al*., 2007), the larger availability of fruits also requires a lower energy investment during foraging when compared with other food items, such as fish or macroinvertebrates. For *A. nuchalis*, the lack of distinctiveness in feeding strategies between hydrological seasons is due to the prevalence of feeding on aquatic invertebrates during the most of hydrological periods, except for ebb and dry of 2012. We believe that the more generalist feeding habit of *A. nuchalis* may balance the energy investment in foraging required during active searches for aquatic insects and crustaceans.

The amount of food eaten by *A. nuchalis* and *T. piresi* reinforces the distinct trophic behavior between these two auchenipterids. *Auchenipterus nuchalis* increased feeding intensity during the dry and ebb seasons, the period of which aquatic insects and/or crustaceans have their density and distribution limited to the river channel (Junk *et* *al*., 1989), which may facilitate their capture by these predators. Although this pattern is often described for piscivorous species (Luz-Agostinho *et al*., 2008; Prudente *et al*., 2016; Barbosa *et al*., 2018), it can be extrapolated for aquatic invertebrate's feeders. On the other hand, *T. piresi* showed a higher feeding intensity during the flood season due to a greater intake of seeds and fruits. Well-documented studies report the relationship between terrestrial plant fruits and fish diet (Freitas *et al*., 2011; Correa, Winemiller, 2014). During the high-water periods occur the fruitification of many floodplain trees (Maia, Jackson, 2000; Ferreira, Parolin, 2007), which are frequently eaten and dispersed by fishes (Correa, Winemiller, 2014; Freitas *et al*., 2018).

The present study highlights that many aspects of the fish ecology are influenced by the natural flood pulse, making it challenging to plan a general prediction of the impacts on local river hydrological alterations (*e.g*., by dams and removal of riparian vegetation) (Junk *et al*., 1989; Bayley *et al*., 2018). Even within a single taxonomic group, such as Auchenipteridae, we evidenced heterogeneity of ecological strategy in response to the flood pulse. Consequently, these species take part in different ecosystem functions, which need to be considered when discussing biodiversity and ecosystem conservation.

In this context, we believe that *A. nuchalis* and *T. piresi* present different responses to the environmental changes caused by the Belo Monte Dam built concluded in November 2015. In general, river damming results in many negatives disturbs in aquatic ecosystems dynamic such as water flow changes, blocks animal movements, disrupts downstream transport of nutrients, softening of the seasonal foods, and decreasing floodplains productivity (Castello, Macedo, 2016; Winemiller *et al*., 2016). For the fish fauna, the reduction of the flood pulse dynamic in the dam reservoir may diminish the availability of seeds and fruit for frugivorous populations (*T. piresi* in our case), as well as threaten seed dispersal processes (Galetti *et al*., 2008). There is a better chance that aquatic insects and crustaceans will maintain their population dynamics (Principe, 2010; Piniewski *et al*., 2017) and their availability for invertivorous organisms. However, there is already evidence of a decline in the abundance and diversity of aquatic insects because of environmental changes caused by river damming (*e.g*., physical-chemical parameters of water) (Romero *et al*., 2021). Such adverse effects in fish populations have been reported for the Tucuruí reservoir (Tocantins River), where *A. nuchalis* is still frequently collected, and *T. piresi* is one of the species considered locally extinct (Mérona *et al*., 2001). Finally, we emphasize that studies considering the relationship between flood pulse and feeding ecology of the organisms are essential to better understand the dynamics of river-floodplain systems. It becomes even more crucial considering the current habitat modifications that are continually being planned in many South American river basins (Winemiller *et al*., 2016).

Thus, besides filling existing knowledge gaps on the ecological relationships between fish species and the environment, our findings also highlight the potential impacts on aquatic systems caused by the Belo Monte and could be used in future comparisons and conservation and management of regional fish species. We also encourage further research in the study area to track and elucidate the effects caused by the Belo Monte in the fish diet and their population dynamics.

All in all, our results demonstrate that a seasonal variability of the diet of two auchenipterid catfishes may be linked to the flood pulse. However, the hydrological variations may be causing different effects on the feeding ecology of these two phylogenetic-related fish species. Even though the flood pulse affects the diet composition of both species, the feeding strategy (niche breadth) and feeding intensity of *A. nuchalis* were not affected by the local flooding dynamic and showed a more generalist feeding strategy than *T. piresi*. The more significant influence of the Xingu River flood pulse in the feeding ecology of *T. piresi* over *A. nuchalis* also allows us to infer about distinct responses of the species to anthropogenic disturbances on the natural hydrological regimes, such as the construction of the Belo Monte dam. To better understand the resistance capacity of these populations to anthropogenic disturbance requires the knowledge of many other ecological aspects, such as behavior and interspecific relationships, which should be considered in future studies.

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AUTHORS' CONTRIBUTION

Tiago Magalhães da Silva Freitas: Conceptualization, Formal analysis, Methodology, Writing-original draft, Writing-review and editing.

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Luciano Fogaça de Assis Montag: Funding acquisition, Project administration, Writing-review and editing.

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The authors declare no competing interests.

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